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Universal Biomass and Energy Flow Distribution in Weighted Food Webs

Yuanjing Feng, Jiang Zhang*

Department of Systems Science, School of Management, Beijing Normal University, Beijing 100875, China

Abstract

Previous studies on food webs always neglect weight information of edges and nodes. However, as the empirical food webs collected by researchers indicate that not only topological structures, but also weight information of each edge and vertex is available, in which, edge weight is the energy flux between any two species, and vertex weight is the total biomass of a given species on the food web. We define two variables F_i and B_i for each species i representing the total energy flux through i and the total biomass of it respectively. Then we find following common patterns of these variables by investigating 20 empirical weighted food webs: (1) F_i and B_i all follow DGBD distribution (with two exponents a and b) which is a kind of deformed Zipf law; (2) A power law relationship $B_i \sim F_i^{\tau}$ with an exponent τ in [0.63, 1.75] is always held for all the empirical webs. This relationship can be viewed as the counterpart of the Kleiber's 3/4 allometric scaling law in the population level. Finally, several mathematical relationships among the exponents a,b in both distributions and τ are derived and tested against the empirical food webs.

Keywords: Weighted food webs; Biomass distribution; Energy flow distribution; Allometric scaling.

* Corresponding author. Tel.:+86-010-58802732, Fax: +86-010-58807876
E-mail address: zhangjiang@bnu.edu.cn.

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1. Introduction

Weighted complex network (e.g. air traffic networks and metabolism networks) can reveal some unique patterns and features which are never found in binary ones [1]. Complex food web is a powerful tool for ecological studies of a large number of species as an interacting system, however, previous studies past have often overlooked in weights of nodes and edges. In this paper we discuss weighted food webs, in which, the edge's weight is the amount of energy flow from one species to another, and the node weight is the biomass of a species correspondingly.

Lots of previous studies have been made for discussion of energy flow networks in ecosystems [2]. In order to depict the macro-state of energy flows in ecosystems, many systematic indicators have also been designed [3, 4] , of which some can not only reflect the direct energy flows between species but also indirect effects and inter-dependence of species [3, 5]. Although some important discoveries about the general structure and function of ecological networks were made [3, 6, 7-10], few of them focused on the energy flow or biomass distributions [11].

This paper will reveal the underlying heterogeneities and universal scaling behaviours of food webs. At first, we define two variables F_i and B_i for each node (species) i, where F_i is the total energy flux through i and B_i is the total biomass of it. By fitting the distributions of F_i and B_i, we adopt a new function which is called DGBD (discrete version of a generalized beta distribution) curve [12]. This function can fit the rank-ordering distribution curves of F_i and B_i very well by tuning three variables A, a and b. The main reason for choosing this function is the fitting goodness of this function is much higher than the classical Zipf distribution (R^2 is always 0.95). This will be discussed in detail in section 2.4.

After that, we also find the power law relationship between F_i and B_i. This power law relationship reminds us the famous allometric scaling law [13-15]: Kleiber [16] revealed that the metabolism and body size of an organism usually follow a ubiquitous power law relationship with an exponent around 3/4. Here, if we treat the whole population of a species as an integrated organism, F_i and B_i are its metabolism and body mass respectively So the power law relationship between F_i and B_i is comparable to the famous 3/4 law, however, the exponent τ is not 3/4 anymore in our study (see Section 3.3).

Finally, a simple relationship between the exponents in biomass and energy flux distributions and the power law relationship of F_i and B_i is derived mathematically and tested by the empirical food webs in Section 3.4.

2. Methods

2.1 data source

We have investigated the 20 food webs in different ecological environments, the food web information including node (species), node intensity (species biomass), edge (energy flow relationship not the feeding relationship), and weight of an edge (energy flux). The energy flux between two species was measured as the unit volume flow of the carbon element into or out of the species (the unit is $gC/m^2/year$)). And the biomass stands for the total mass of living biological organisms of a species in a certain period of time and per unit volume, customarily it was also measured by carbon content (the unit is gC/m^2) [17]. These food webs' information is obtained from an online database (url: http://vlado.fmf.uni-lj.si/pub/networks/data/bio/foodweb/foodweb.htm), most of them are from published papers. In Table 1, we list the name and the number of nodes N and edges E in each web.

2.2 flux matrix

Our work is based on the flux matrix of a weighted food web. An ecological energy flow network is a weighted directed graph that represents relationships of ecological energy transfer between species. This graph can be represented by a matrix which is called flux matrix in this paper:

$$F_{(N+2)\times(N+2)}=\{f_{ij}\}_{(N+2)\times(N+2)} \quad (1)$$

Where f_{ij} is the energy flux from species i to j. Two special nodes representing the environment: node *0* and node *N+1* are added to the web. Node *0* denotes the source of energy flow, whereas node *N+1* represents the sink. We expect that the dissipative and exported energy will flow to the node *N+1*. Therefore, there are in total $(N+2)\times(N+2)$ entries in the flux matrix. This matrix can be read from the original weighted food webs [17].

Table 1. The list of food webs (N is the number of nodes and E is the number of edges)

Food web	Abbre..	*N*	*E*
Crystal River Creek (Delta Temp)	CrystalD	24	100
Crystal River Creek (Control)	CrystalC	24	125
Chesapeake Bay Mesohaline Net	Chesapeake	39	177
Lower Chesapeake Bay in Summer	ChesLower	37	178
Middle Chesapeake Bay in Summer	ChesMiddle	37	209
Upper Chesapeake Bay in Summer	ChesUpper	37	215
Narragansett Bay	Narragan	35	220
Lake Michigan	Michigan	39	221
St. Marks River (Florida)	StMarks	54	356
Mondego Estuary - Zostrea site	Mondego	46	400
Cypress, Wet Season	Cypwet	71	631
Cypress, Dry Season	Cypdry	71	640
Everglades Graminoids, Dry Season	Gramdry	69	915
Everglades Graminoids, Wet Season	Gramwet	69	916
Everglades Graminoid Marshes	Everglades	69	916
Mangrove Estuary, Dry Season	Mangdry	97	1492
Mangrove Estuary, Wet Season	Mangwet	97	1492
Florida Bay, Wet Season	Baywet	128	2106
Dry Season Florida Bay	Baydry	128	2137
Florida Bay,	Florida	128	2106

2.3 Variables Fi and Bi

We will calculate the total flux through any given node *i* according to the flux matrix ***F***. This value is also called node intensity in complex weighted network studies [18]. Because the network is always balanced, we need only to calculate the efflux of each node as F_i,

$$F_i = \sum f_{ij} \quad , \quad 1 \leqq i \leqq N \tag{2}$$

In addition, we define another variable to represent the intensity of a node, B_i, indicating the biomass of *i*. This information is also available from the original weighted food webs.

2.4 Distributions and DGBD curves

We will study the distributions of F_i and B_i in any empirical food web. Instead of giving the empirical density function or distribution function of F_i and B_i [11], we use the rank-ordering curve to show the distributions of these two variables. For example, if we have a small food web with 5 species, and their biomass values are {100, 19, 200, 5, 1} gC/m^2. Then we can rank these values in a decreasing order to get a sequence: {200,100,19,5,1}. We plot this sequence on a coordinate with the horizontal axis as the rank value, namely {1,2,3,4,5} and the vertical axis as the biomass values. So the final curve on this coordinate

is the rank-ordering curve. The main advantage of using the rank-ordering curve is its simplicity of the calculation. Actually, as long as we rank all the F_i or B_i values according to the decreasing order of nodes, we can obtain the rank-ordering curve. Furthermore, the rank-ordering curve and distribution function contain the same information [19].

Then, we use the DGBDcurve to fit the rank-ordering curves of F_i and B_i:

$$f(r_i) = A\,(N+1-r_i)^a / r_i^b. \quad (3)$$

Where, $f(r_i)$ is the value of F_i or B_i of the node i, and r_i is the rank of i according to F_i or B_i values in a decreasing order. N is the total number of nodes(species) in the food web. A, $a>=0$ and $b>=0$ are parameters to be estimated. A stands for the magnitude of flux or biomass in this food web. a and b are exponents of power laws in the tail and the head of the curves respectively. If we set $a=0$, then formula (3) becomes $f(r_i)=A/r_i^b$, which recovers the famous Zipf law [20]. However, the classic Zipf law is not always the best choice in fitting empirical data because there are large deviations in the tail of the rank-ordering curves [12]. This disadvantage can be mended by introducing a new exponent a in the DGBD rank-ordering curve. In fact, formula (3) can fit lots of empirical data very well [12].

2.5 Power law relationship

In the 20 empirical weighted food webs, we find that F_i and B_i always satisfy a power law relationship:

$$B_i = c\,F_i^{\tau}\ , \quad (4)$$

where exponent τ and c are parameters to be estimated. This relationship can be also viewed as the allometric scaling law because F_i represents the metabolism and B_i is the equivalent body-mass of the whole population of species i in a food web once we treat the whole population as one organism. Thus, this power law relationship is comparable with the famous Kleiber law [16].

3. Results

3.1 The distribution of Fi

We calculate the distribution of F_i for each of the 20 empirical food webs, and fit them by DGBD curves. Four selected food webs are plotted in Fig. 1 in which the red curves are best fitting DGBD functions.

From Fig.1, we know that the best fitting DGBD curves are divided into three parts by two inflexion points, and each part obeys independent logarithmic decreasing behaviour. Obviously, the head and tail parts of the curve have much steep slopes than the middle part. We know that the local slope of the curves reflects the heterogeneity of the energy flux distribution. In other words, the larger the absolute value of slope is, the higher degree of heterogeneity of the vertex correspondingly is. Therefore, we can conclude the result that the nodes in the heads and tails of the curves are more heterogeneous than the ones in the middle parts.

In Fig. 1, we distinguish nodes by their trophic levels. Blue circles, green squares and black stars represent the species on the first, second and third trophic levels respectively. It is observed that the nodes of the first trophic level almost locate the heads, while the species of the second level locate both the heads and the tails, and most the third trophic level species locate in the middle parts. We may conclude that the distribution of energy flux on the second trophic level is much more even than the first and third trophic levels.

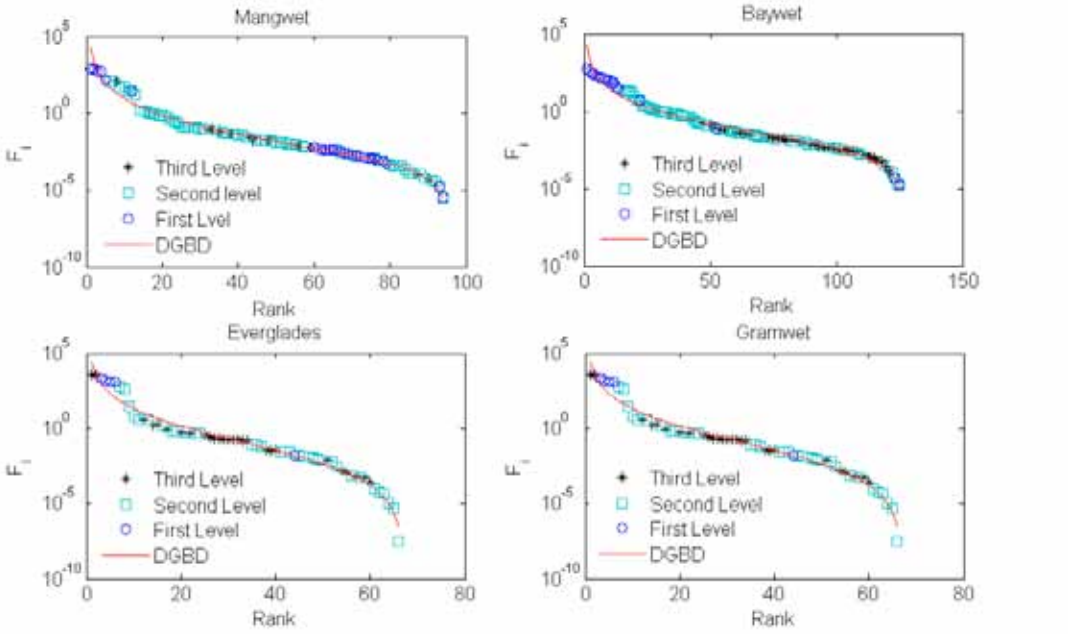

Fig. 1. The rank-ordering curves of F_i and DGBD fittings of four selected food webs.All the curves are on log-linear plots. The points with different markers and colors correspond to different trophic levels.

In Table 2, we list all the fitting parameters and goodness for the 20 webs. By comparing different rows, we know that the food webs with more edges can be better fitted by DGBD curves because their R^2 are larger. Notice that there are three food webs (ChesLower, ChesMiddle and ChesUp) having exponents $b=0$. That means the distributions of F_is for these webs cannot be fitted by DGBD functions very well.

3.2 The distribution of Bi

The same approach can be applied to B_i's. We ignore the rank-ordering curves of B_i's and only list the estimated parameters and the R^2 indicators in Table 3 (the parameters are denoted as A',a' and b' to distinguish the ones in Table 2). Comparing the parameters (A',a',b') in Table 3 and the corresponding ones (A,a,b) in Table 2 for each food web, we can find that they are positive correlated. This correlation encourages us to investigate the relationship between F_i and B_i.

3.3 Allometric scaling relations

According to the similarity between Table.2 and 3, it is easy to find that there exist some connections between random variables B_i and F_i. The plot of these two variables on a log-log coordinate reveals that the relationship between B_i and F_i, is actually a power law. As shown in Fig. 3, the sample points aggregate around their fitted lines very well. This relationship is ubiquitous for all 20 food webs as shown in Table 4.

We use the ordinary linear regression method to find the best fitted lines (Table 4). Most R^2's are larger than 0.8. The R^2's and exponents decrease with the scale of the network because the statistical significance decreases as the number of samples declines.

Note that the exponent τ is not a constant but fluctuate in between [0.6311, 1.7522] for different food webs. The bigger the exponent is the larger the rate of the biomass increasing to the energy flux is. Thus, we can treat the exponent τ as a coefficient of energy flux to biomass transfer rate of the whole food web.

Table 2 All the DGBD fitting parameters of F_i in20 empirical food webs. The rows are sorted according to the number of nodes (N) of the web

Food web	N	E	A	b	a	R^2
CrystalD	24	100	15917.91	4.1523	0.1667	0.9568
CrystalC	24	125	4008.611	3.5536	0.5399	0.9583
Chesapeake	39	177	88.77455	1.5435	2.9333	0.9422
ChesLower	37	178	4.81E-06	0	6.0882	0.8401
ChesMiddle	37	209	0.004285	0	3.9974	0.8533
ChesUpper	37	215	0.03545	0	4.0626	0.8603
Narragan	35	220	493412.1	2.5378	0.8016	0.9302
Michigan	39	221	8.82E-05	1.2335	5.3117	0.8893
StMarks	54	356	5.44937	1.3286	1.2456	0.9851
Mondego	46	400	0.013309	1.7001	3.3649	0.9664
Cypwet	71	631	12.18493	2.629	2.7436	0.9647
Cypdry	71	640	0.21994	2.3608	2.3402	0.9546
Gramdry	69	915	2.99008	3.1755	2.0823	0.975
Everglades	69	916	0.079412	2.9437	3.0259	0.9694
Gramwet	69	916	0.053062	2.8428	3.0033	0.9717
Mangdry	97	1492	18.08531	3.2204	1.51	0.9743
Mangwet	97	1492	11.28416	3.3195	1.6703	0.9776
Baywet	128	2106	7.076646	2.7996	1.6464	0.9748
Baydry	128	2137	7.076646	2.6286	1.62	0.9752
Florida	128	2106	3.948754	2.7996	1.6464	0.9748

3.4 Relationship of scaling exponents

We have discussed the distributions of F_i and B_i in Section 3.1 and 3.2, so we can get the following equations:

$$F_i = A\,(N+1-r_i)^a / r_i^b \qquad (5)$$

and

$$B_i = A' (N+1-r_i)^{a'}/r_i^{b'} \quad (6)$$

for each node i. As we have shown, F_i and B_i are random variables following (5) and (6) with three pairs of parameters A, a, b and A', a', b' respectively. F_i and B_i also follow a power law relationship with the parameters τ and c in equation (4). If we bring equation (5) and (6) into equation (4), we can easily derive the following equation:

Table 3 All the DGBD fitting parameters of Bi in 20 empirical food webs. The rows are sorted according to the number of nodes (N) of the web

Food web	N	E	A'	b'	a'	R^2
CrystalD	24	100	1208270	4.3003	0.1125	0.9663
CrystalC	24	125	380103.9	3.8878	0.2384	0.9473
Chesapeake	39	177	262.9858	2.1689	1.6963	0.9903
ChesLower	37	178	0.000148	0.753	5.525	0.8458
ChesMiddle	37	209	0.143603	0.7713	3.4207	0.8673
ChesUpper	37	215	0.179012	0.8613	3.4186	0.8773
Narragan	35	220	23144.21	1.8828	0.1602	0.927
Michigan	39	221	1.26E-06	0.181	4.7955	0.8893
StMarks	54	356	1521.725	2.1413	0.9392	0.9752
Mondego	46	400	3.062097	2.4303	1.4119	0.9872
Cypwet	71	631	2.909264	4.2314	3.029	0.9786
Cypdry	71	640	1.567058	3.9924	2.515	0.9767
Gramdry	69	915	0.005721	2.7487	2.7472	0.9659
Everglades	69	916	8.28E-05	2.4015	3.7411	0.969
Gramwet	69	916	9.07E-05	2.4441	3.7559	0.9708
Mangdry	97	1492	17.73252	4.0846	1.4067	0.9843
Mangwet	97	1492	8.372897	4.1792	1.6281	0.9854
Baywet	128	2106	0.004718	2.4016	2.2586	0.9872
Baydry	128	2137	0.003459	2.2779	2.2366	0.9786
Florida	128	2106	0.004718	2.4016	2.2586	0.9872

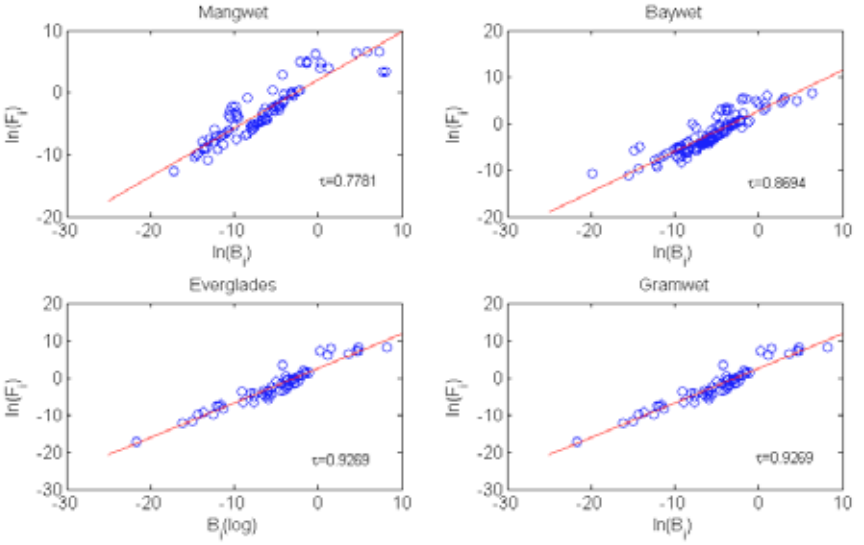

Fig.2. The power law relationship between Fi and Bi for four selected food webs

Table 4 The power law relationships between Fi and Bi for all 20 food webs. The rows are sorted according to the number of nodes (N) of the web

Food web	*N*	*E*	*c*	*τ*	R^2
CrystalD	24	100	2.9949	0.9596	0.9383
CrystalC	24	125	-2.5545	0.9037	0.9264
Chesapeake	39	177	3.7243	1.0328	0.7477
ChesLower	37	178	-2.0934	1.7522	0.9099
ChesMiddle	37	209	-0.8018	1.5776	0.8166
ChesUpper	37	215	1.1335	1.2086	0.6372
Narragan	35	220	2.0495	1.1723	0.5473
Michigan	39	221	3.1196	1.1956	0.9428
StMarks	54	356	-1.1246	0.6886	0.7023
Mondego	46	400	2.5736	1.2434	0.866
Cypwet	71	631	1.1585	0.6579	0.7848
Cypdry	71	640	1.1908	0.6311	0.7577
Gramdry	69	915	2.2313	0.9041	0.8951
Everglades	69	916	2.4274	0.9269	0.9171
Gramwet	69	916	2.5226	0.9929	0.821
Mangdry	97	1492	1.9711	0.7748	0.8154
Mangwet	97	1492	1.9713	0.7781	0.8253
Baywet	128	2106	2.6473	0.8694	0.8103
Baydry	128	2137	2.4585	0.8536	0.8117
Florida	128	2106	2.6473	0.8694	0.8103

$$A\,(N+1-r_i)^{a} / r_i^{b} = c\,(A'\,(N+1-r_i^{a'} / r_i^{b'})^{\tau} \quad (7)$$

This will be always held for any r_i. So comparing the coefficients of the terms $(N+1-r_i)$ and r_i, we can derive the following relationships.

$$A = c\,A'^{\tau}, \quad (8)$$

And

$$a = a'\,\tau \quad (9)$$

$$b = b'\,\tau. \quad (10)$$

Equation (9) and (10) are more important than equation (8) because the exponents a,b and a',b' characterize the shapes of the distributions which can account for the heterogeneity of the energy flux or biomass. So we test equation (9) and (10) by calculating the relative errors of the predicted relationships between the exponents for all food webs in Fig.3.

From Fig. 3, we know that the relative errors of both a and b almost decrease as the scale of the network. As the distributions or power law relationships are statistical properties, the significances of these regularities will increase with the number of samples. Therefore, the features of food webs that we have studied in this paper are more obvious and accurate for large networks since larger webs have more sample points. Another point should be noted is the relative errors of b for the three food webs with $b=0$ (ChesLower, ChesUpper and ChesMiddle) are ignored in Fig.3 because they go infinity.

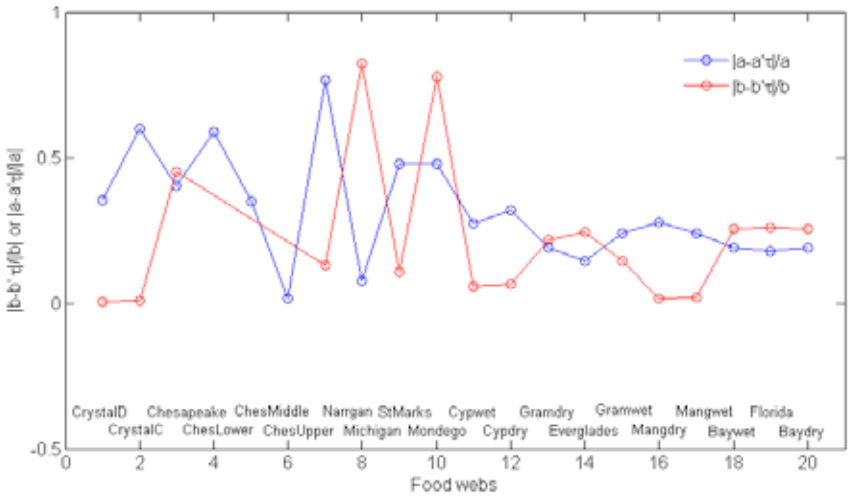

Fig.3. The relative errors of the relationships among exponents for all 20 food webs (The food web names are listed on the bottom of the figure. The three points with b=0 are ignored because the relative errors go infinity for these three webs).

4. Conclusion

Now, the weight information of nodes and edges on food webs is available, however, very few studies focus on these weights. In this paper, we study the distributions of node weights as biomass of the species and the weight intensity of each node as the total energy flux transferred by the species.

We find that both F_i and B_i follow DGBD rank-ordering distribution. That indicates the heterogeneity of the energy flux and biomass distribution cannot be ignored. By plotting the trophic levels on the distribution curves, we find that the species in the second trophic level can share the energy flux and biomass more evenly than the other levels.

Furthermore, we also study the relationship between F_i and B_i. A power law relationship $B_i \sim F_i^{\tau}$ with an exponent τ in [0.63, 1.75] is found in our empirical food webs. This relationship can be viewed as the counterpart of the Kleiber's 3/4 allometric scaling law in the population level.

Finally, several mathematical relationships among the exponents a,b in both distributions and τ are derived and tested against the empirical food webs. We reveal that the universal distributions and relations are more accurate for large size food webs than the small ones.

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